

POPULATION ESTIMATES FOR THE WANING YEARS OF THE PACIFIC SARDINE FISHERY

ALEC D. MACCALL
California Department of Fish and Game
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

New sardine (*Sardinops sagax caerulea*) population estimates for the period 1945 to 1965 are calculated based on a cohort analysis of aged landings data. Three-year-old fish were incompletely recruited after 1953, requiring assumption of age 4 as age of full recruitment. The assumed natural mortality rate (M) was maintained at 0.4 for the entire time series. Landings from waters south of Punta Baja, Baja California, were excluded from the analysis. Biomass estimates are smaller than those previously given but agree well with independent indices of abundance. The new ratio of sardine spawning biomass to CalCOFI sardine larva census is double the previous value. A 95% confidence interval ranges from one quarter to quadruple the estimated biomass. The stock-recruitment relationship shows no curvature for the entire time series taken as a whole, and a purely functional description of the relationship is that mean recruitment only slightly exceeds potential replacement of spawners at all levels of abundance. Population simulations demonstrate this lack of resilience to fishing. Maximum constant fishing pressure that the population could have sustained was about 22% per year ($F = 0.25$). Maximum sustainable yield was about 250,000 tons/year, which is far below previous estimates.

INTRODUCTION

Estimates of Pacific sardine (*Sardinops sagax caerulea*) spawning biomass in California waters for the period 1932 to 1957 were made by Murphy (1966) using cohort analysis. Besides being the basis of most present analyses of the dynamics of the sardine fishery, estimates of spawning biomass from 1951 to 1957 have been used to calibrate larva surveys for estimation of northern anchovy (*Engraulis mordax*) spawning biomass (Smith 1972). As the northern anchovy fishery is now beginning to expand to a level where increased precision in management is necessary, improvement of the anchovy data base is desirable, and therefore, improvement of the sardine population estimates is indicated.

Murphy offered his analysis of the 1952-1960 seasons as a tentative solution and intended that "As more information . . . becomes available, the solution . . . can be re-examined." The last season for which the age composition of the sardine landings was published is 1965, which was also the last year of significant landings in California.

Murphy used landings up to 1960, so the usable time series can be extended another five years by updating his analysis. Other aspects of Murphy's analysis can also bear revision, particularly with regard to the present use of the results, that of anchovy biomass estimation. Murphy showed that a natural mortality rate of $M = 0.4$ is our best estimate, but for the time series subsequent to 1950, he preferred to double this value to $M = 0.8$ in order to obtain a trend in population sizes which agreed with the egg counts obtained from CalCOFI surveys. Since we are now using Murphy's estimates to calibrate those surveys, the process is suspiciously circular, and consistent use of the best estimate of $M = 0.4$ will preserve independence of the data sets. Age of full recruitment is another assumption that can bear examination and possible revision. Finally, Murphy included the Cedros Island catch in his landings data, which undoubtedly included large amounts of fish from the southern sardine stock that may never have been available in California. Since the northern anchovy central subpopulation has a southern boundary in the vicinity of Punta Baja, Baja California, estimation of biomass by comparing anchovy and sardine spawning products requires that the sardine biomass estimates be based on a similar area. Only sardine landings presumably caught north of Punta Baja will be considered in this analysis.

DATA

The basic input data to a cohort analysis are aged landings (Table 1). For the seasons before 1951, the catch data in Murphy's Table 13 are used. For the period 1951 to 1960, aged landings were recalculated from information in Wolf (1961) and from estimates of total tonnages landed in various regions of the fishery (Table 1). Age compositions for the 1961 to 1965 season were obtained from the individual landings reports (Daugherty and Wolf 1964; Kimura and Blunt 1967; Blunt and Kimura 1966; Kimura and Blunt 1971; Blunt and Kimura 1971; listed in order). Aged landings for each region were modified according to revised total tonnages obtained from various sources. In the late 1950's and early 1960's, sardine catches made out of season (i.e. in the "inter-season") were not included in the landings reports, so aged landings were increased according to the tonnages reported in the California Department of Fish and Game Marine Fish Catch Reports. The aged landings for 1965-

TABLE 1
 Pacific Sardine Landings.

Season	Landings (short tons)				Aged landings (1,000 fish)						
	Central California	Southern California	North Baja California	Total	O	I	II	III	IV	V+	Total
1950-51*	46,426	306,662	-	353,088			1,129,439	996,899	391,172	90,704	2,608,214
1951	15,679	113,125	16,022	144,826		13,908	69,624	778,877	179,837	79,603	1,121,849
1952	49	5,662	7,971	13,682		871	4,604	20,533	50,771	17,020	93,799
1953	58	4,434	12,303	16,795		2,150	5,928	35,025	10,812	49,606	103,521
1954	856	67,609	11,694	80,159	3,833	3,011	203,058	228,849	72,644	113,525	624,920
1955	518	73,943	3,828	78,289		11,340	71,827	268,656	140,996	57,483	550,302
1956	63	33,580	12,290	45,933			20,080	90,154	115,587	41,410	267,231
1957	17	22,255	8,932	31,204	4,393	56,544	57,910	77,527	35,141	41,120	272,635
1958	24,701	79,270	16,527	120,498		131,713	812,293	252,062	37,556	23,653	1,257,277
1959	15,645	21,538	14,140	51,323		67,723	299,484	150,980	18,231	2,112	538,530
1960	2,076	26,690	10,148	38,914		3,523	107,991	164,380	56,161	4,457	336,512
1961	2,211	23,313	1,587	27,111	1	369	11,029	34,613	76,001	45,837	167,850
1962	1,206	2,897	2,592	6,695		6	2,290	13,814	15,827	10,608	42,545
1963	1,008	2,459	2,521	5,988		1,458	4,332	9,202	13,291	11,347	39,630
1964	307	5,984	476	6,767	98	274	7,591	21,838	12,442	10,631	52,874
1965	70	909	431	1,410			730	523	2,250	4,765	8,268

*Landings prior to 1950 are as reported in Murphy (1966).

66 were poorly sampled and incomplete; therefore for this season the southern California age composition was assigned to all California landings and the Baja California interseason age composition was assigned to all Baja California landings. The amount of fish caught in northern Baja California waters before 1961 was estimated by multiplying the Baja California tonnage by the combined Ensenada and San Quintin percents of total landings in Murphy's Table 7. For 1961 through 1963, Murphy's Table 8 was used in similar fashion. The 1964 and 1965 landings reports say that "insignificant" amounts of the sardines processed in Ensenada were caught locally, which I have interpreted as 10%, for lack of a better estimate.

In most of the aged landings reports, no distinction is made between Cedros Island-area catch and Ensenada-area catch, which becomes a problem in 1961 through 1965, when large amounts of fish caught in central Baja California were shipped to Ensenada for processing and appear in the Ensenada landings estimates. Length frequencies for the two areas differ considerably in some years, with Ensenada fish being generally smaller than southern California fish and with Cedros Island fish being smaller yet (Blunt and Kimura 1966; Kimura and Blunt 1967). Two sets of landings data for 1961 to 1965 were analyzed separately, one assigning the Baja California age composition to the Ensenada catch, and the second assigning the southern California age composition to the Ensenada catch. As the true Ensenada age composition is likely to be intermediate between the two estimates, the estimates made by separate cohort analyses should correspondingly bracket the estimate that would have been obtained using the true Ensenada age composition.

ESTIMATION OF FISHING MORTALITY RATES

Cohort analysis, as described by Tomlinson (1970), was used to estimate fishing mortality rates from the aged landings data. Natural mortality is assumed to be $M = 0.4$, based on the review of sardine natural mortality rate given by Murphy (1966). Age 4 and older fish are considered fully recruited, so catch ratios of the form

$$R_i = \frac{\sum_{j=5}^{\infty} C_{i+1,j}}{\sum_{j=4}^{\infty} C_{i,j}}$$

where i is fishing season, and j is age, were used to connect the time series of fully recruited ages. A backward solution estimated F_i , given F_{i+1} and R_i , and due to the assumption of full recruitment, the F_i so estimated for age-4+ fish was assigned to the age-5+ fish in the same season, allowing the process to be repeated for the next earlier cohort. The assumption of full recruitment at age 4 was necessitated by that being the oldest age for which older fish were still sufficiently abundant to obtain catch ratios that were relatively unaffected by sampling variation. Solution for the younger, partially recruited ages was also done by the method described by Tomlinson (1970). Murphy's solutions were based on mathematically equivalent calculations; therefore, the method itself is not a source of difference in the results given here.

The fishing mortality rate for fully recruited ages in 1965 was arbitrarily set at $F_{1965} = 0.6$ to initiate the time series. Since this is purely a guess, the 1965 and 1964 values must be considered inaccurate. Fortunately, backward solution has the property of convergence (Tomlinson 1970; Jones 1961), wherein each successive earlier estimate is less affected by error in later estimates and tends toward a fixed value, which can be called its

true value if all assumptions are valid. Thus, the F_i estimates for $i = 1963$ and earlier may be considered to be reasonably independent of the initial guess.

For the 1950's, fishing mortality rates estimated from the new data and assumptions tend to be two to three times larger than those estimated by Murphy (Table 2). After 1953, 3-year-old fish are not fully recruited, averaging 69% the fishing mortality rate of older fish from 1954 to 1963. Violation of the assumption of full recruitment caused progressive underestimation of F for "fully recruited" ages in Murphy's solution. This also explains why Murphy had to choose an inordinately large value of M and of F_{1960} to initiate his solution. The present solution gives results back to 1945, where the recalculation converges with Murphy's solution. Both previously discussed methods of assigning age composition to the later Mexican catches give approximately the same results (Table 2), except for the younger ages after 1961.

An additional factor tending to keep Murphy's estimates of fishing mortality low is his inclusion of catches from the more lightly exploited southern stock in central Baja California. As these southern landings become an

TABLE 2
 Pacific Sardine Fishing Mortality Rates.

Age Season	$M = 0.4$			Murphy (1966) $M = 0.4$		Murphy (1966) $M = 0.8$	
	2	3	4+	2	3+	2	3+
1945-46	0.631	1.017	1.179	0.553	1.170		
1946 ...	0.496	0.752	0.595	0.476	0.589		
1947 ...	0.285	0.415	0.628	0.194	0.389		
1948 ...	0.314	0.313	0.326	0.346	0.192		
1949 ...	0.514	0.669	1.054	0.430	0.619		
1950 ...	0.455	1.148	1.207	0.394	0.796		
1951 ...	0.349	0.880	0.876		0.681	0.039*	
1952 ...	0.014	0.204	0.151		0.113	0.002	0.036
1953 ...	0.007	0.179	0.196		0.143	0.000	0.042
1954 ...	0.229	0.555	0.901		0.340	0.103	0.245
1955 ...	0.257	0.691	1.108		0.203	0.118	0.376
1956 ...	0.096	0.773	1.002			0.044	0.431
1957 ...	0.127	0.841	1.113			0.014	0.476
			(1.112)†				
1958 ...	0.922	1.790	2.424			0.690	1.218
	(0.916)	(1.783)	(2.417)				
1959 ...	0.503	0.553	0.808			0.406	0.783
	(0.501)	(0.546)	(0.798)				
1960 ...	0.592	0.756	0.528				1.359
	(0.565)	(0.752)	(0.516)				
1961 ...	0.128	0.490	1.440				
	(0.086)	(0.388)	(1.465)				
1962 ...	0.038	0.292	0.562				
	(0.002)	(0.358)	(0.445)				
	(0.149)	(0.079)	(0.683)				
1964 ...	1.549	1.353	0.896				
	(2.145)	(1.739)	(0.932)				
1965 ...		0.5	0.6				

*Estimated from Murphy's (1966) Tables 13 and 14.

† Parentheses indicate results of assigning southern California age composition to the Mexican landings in seasons 1962 through 1965.

increasing fraction of the total catch, the age composition of the southern stock, which reflects less fishing mortality, progressively dominates the cohort analysis, producing underestimated F and overestimated population size for the northern fishery.

ESTIMATION OF BIOMASS

Murphy's (1966) procedure was followed as much as possible, but information on actual weights of individual age groups in the catch compositions is lacking, forcing the use of approximate methods. Since total catch weight and landings by age in number are known (Table 1), age groups were assigned the weights at age given in Murphy's Table 17, and the total catch weight was apportioned by the estimated percentage weight composition, giving estimated landings by age in tons. These landings were then divided by the exploitation rate to give age group biomasses at the beginning of the season. Population biomass was then obtained by summing over age groups (Table 3). Murphy's calculations of spawning biomass for years before 1951 included only half of the 2-year-old fish. The present estimates include all of this age group for the entire time series, under the assumption that 2-year-olds are inherently capable of spawning and therefore constitute a "potential" spawning biomass. This simplification avoids the abrupt change of methods found in the previous estimates. Too little information is available to attempt to define a population size-dependent maturity function.

TABLE 3
 Pacific Sardine Biomass and Recruitments.

Year	Adult biomass (10^6 metric tons)		Recruitment	
	Present calculation	Murphy's (1966) Table 15	Year-class at age 2 (10^6 fish)	Murphy's (1966) Table 14
1945	720	757	2,385	2,620
1946	566	459	1,625	1,680
1947	405	475	1,667	2,349
1948	740	623	3,875	3,102
1949	793	869	4,261	4,921
1950	780	883	5,690	4,151
1951	277	517	290	2,205
1952	136	503	397	2,494
1953	202	643	972	3,380
1954	239	606	1,197	3,011
1955	170	386	382	935
1956	108	266	264	695
1957	90	192	588*	1,216
1958	177	255	1,586*	2,490
1959	122	172	905*	1,327
1960	88		288	
1961	54		111	
1962	27		74	
1963	21		56	
1964	11		11	
1965	3			

*These recruitments are slightly underestimated due to significant catch of fish at age 1.

Biomass estimates for 1951 and later are much smaller than those calculated by Murphy, as is consistent with the estimates of fishing mortality rate. Despite the poor accuracy of the estimates of fishing mortality rate in 1964 and 1965, the biomasses for those years are undoubtedly extremely small relative to previous years. The two methods of assigning age composition to Mexican landings give nearly identical estimates of biomass, so the solution using Mexican age compositions is presented as the final estimate.

DISCUSSION

Availability at Age

As discussed earlier, Murphy's estimates of fishing mortality rates for the 1950's appear to have been biased downward because he included incompletely available 3-year-old fish in his catch ratios for assumed fully recruited age groups. Thus, the new estimates of fishing mortality rates that are based on an older assumed age of full recruitment are considerably higher because most of the catch ratios are smaller (i.e. catches of year-classes show a larger relative decrease in subsequent years). A comparison of relative availability to the fishery, as measured by the ratio of fishing mortality of ages 2 and 3 fish to "fully recruited" age 4+ fish (Figure 1) shows an interesting trend. Until 1953, 3-year-old fish appear to have been nearly fully available. This group subsequently, with the exception of the 1960 season, underwent a decline in relative availability to 70% in the later 1950's and to less than 50% in the early 1960's. Two-year-old fish show an even more severe drop in relative availability, a decline which also started earlier. From an average of 65% relative availability in the late 1940's, 2-year-olds dropped to 10% relative availability in the 1950's and later, with the exception of the warm-water years, 1958-60.

These trends are remarkably consistent with Felin's (1954) hypothesis concerning the geographic origin of year classes in the later years of the fishery, wherein the later, weaker year classes were thought to be of southerly origin. Now we can further hypothesize that as the fish in the catch were becoming predominantly of southern origin, slow rates of migration into California waters resulted in these fish not being fully available until an older age than was experienced from previous locally produced year classes. Oceanic conditions appear to have influenced this immigration rate as in the case of the warm-water years, when strong northward migration of sardines resulted in greatly increased availability of young fish to the southern California fishery.

Egg and larva surveys have shown little spawning in the Los Angeles Bight since 1951, except during the warm-water years (Kramer 1970). This independent

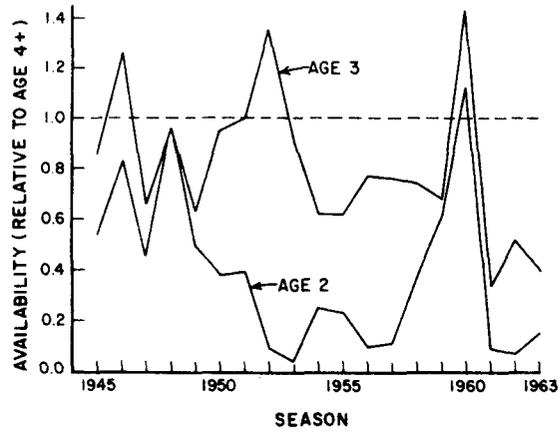


Figure 1. Relative availability of 2- and 3-year-old sardines compared to fully recruited age groups.

source of information strongly supports the above hypothesis, and the occurrence of northerly spawning in the warm-water years also helps explain the high availability of the 1957 and 1958 year classes. At the same time, these conditions of high availability resulted in the fleet generating maximal fishing mortality during this period, with the exploitation rate reaching 80% of fully recruited fish in 1958. It is ironic that the conditions that allowed the fishermen to rejoice at the return of the sardine insured the loss of the fishery by making those same sardines extraordinarily vulnerable to capture.

Biomass

Whereas Murphy's estimates of total biomass (age 2+) show a relatively large population in 1950, dropping to intermediate levels in 1951-1954 and then declining steeply, the present solution shows an extreme drop in biomass after 1950, and a subsequent slower, fluctuating decline (Figure 2). Of course, it must be emphasized that there is a geographic difference between the two population estimates in that the new solution is restricted to the waters north of Punta Baja, approximately the boundary between central and northern Baja California, and that much of the difference in the two solutions may be explainable on this basis alone. However, for examining events in the California fishery, the new solution should be more appropriate. The decline since 1950 has been monitored by three other independent methods, and a comparison of these time series with both Murphy's and the new cohort analysis should be informative. The three independent methods are 1) catch-per-unit-effort (Clark 1956; Klingbeil 1974); 2) night-light surveys carried on by the California Department of Fish and Game (Klingbeil 1974); and 3) egg and larva surveys carried on by CalCOFI.

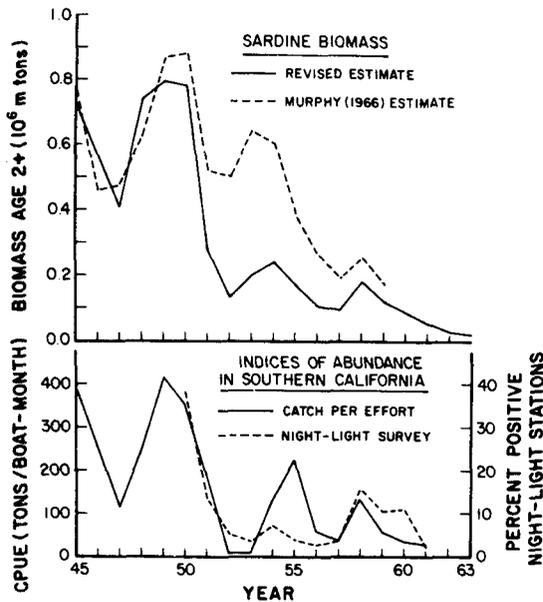


Figure 2. Comparison of sardine biomass estimates and indices of abundance.

Catch-per-unit-effort (CPUE) indices of abundance, particularly when as unrefined as those used in the Pacific sardine fishery, are plagued with systematic errors. MacCall (1976) has shown that the catchability coefficient for available measures of effort in the earlier Pacific sardine fishery tended to vary inversely with biomass, causing decreased sensitivity of CPUE to changes in biomass. Knaggs (1972) documents a wide range of gear improvements in the fishing fleet since 1952. Most of the improvements were in relation to speed and efficiency in the capture and loading of fish. The Puretic power block reduced manpower requirements and operating costs and greatly decreased the duration of a set, allowing more sets to be made on smaller schools. Other improvements resulted in more efficient navigation and location of fish, such as aerial scouting, which takes most of the randomness out of the process of fish location and causes a tendency toward constant CPUE, independent of true abundance. Thus, while CPUE is likely to vary with abundance, it is also likely to underestimate changes in true abundance.

Since most of the landings occurred in the first months of the fishery season after 1944, it is reasonable to compare CPUE with biomass estimates for the beginning of the season. CPUE, in tons per boat-month as given by Clark (1956), and by Klingbeil's (1974) "first approach" (Figure 2), appears to agree somewhat more with the new

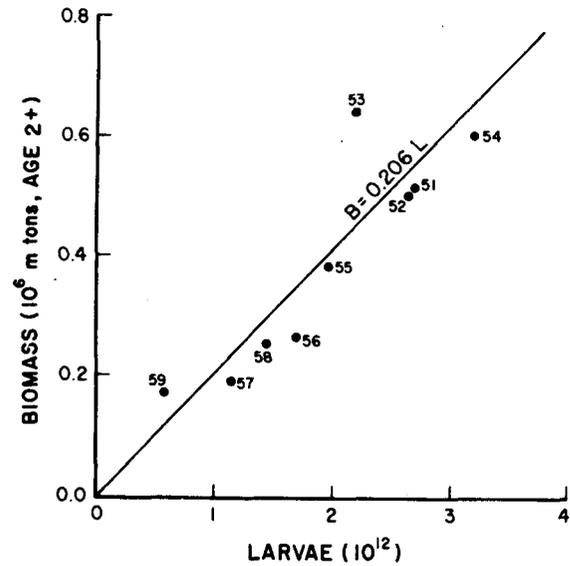


Figure 3. Relationship between sardine spawning biomass and CalCOFI sardine larva census (from Smith 1972).

biomass estimates than with Murphy's estimates. The correspondence is good up to 1952, and the new estimates are much more consistent with the magnitude of the drop in CPUE from 1950 to 1952. The 1953 and 1954 seasons' CPUE are anomalous for both estimates of biomass, although the low fishing mortality rate supports the hypothesis that the stock was not fully available to the fishery. CPUE again agrees well with the new biomass estimates after 1954.

Klingbeil (1974) gives percentage occurrence of sardines at night-light stations as a tentative index of abundance. The index is based on a binomial distribution when fish are abundant, assuming the probability of getting a positive observation is directly related to abundance. However, as abundance becomes small, the probability of obtaining positive observations becomes small, and the distribution becomes approximately Poisson ($N > 100$ and $p < 0.05$), which has the property that the variance is equal to the mean. Thus, the relative precision is poor at low population sizes. Also, pre-recruits accounted for a large number of positive observations, so comparison with abundance estimates is very crude (Figure 2).

Other sources of bias in the night-light index are probable variations in fish behavior, both seasonally and annually. It appears likely that the same factors that may have caused exceptionally high availability of the popula-

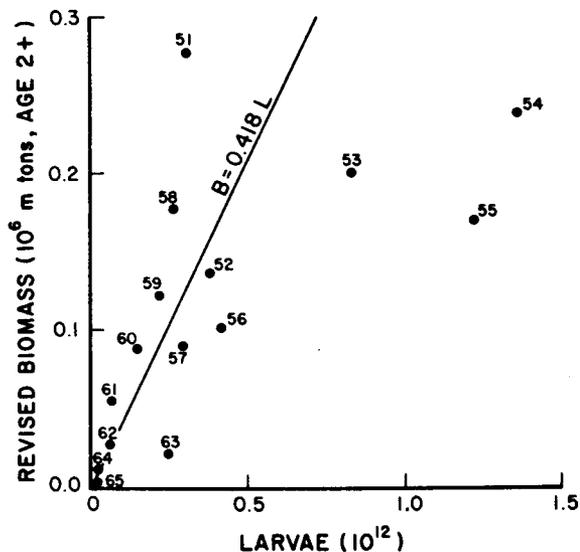


Figure 4. Revised relationship between sardine spawning biomass and CalCOFI sardine larva census for area north of Punta Baja.

tion to the fishing fleet in the warm-water years of 1958-1960 may have resulted in upward bias of the night-light index for those years. Nonetheless, the night-light index shows a large population in 1950, followed by a sharp decline. The 1951, 1954, and 1958 points suggest that abundance in these years may have been on the order of one-third that of 1950, which is much more consistent with the new biomass solution than with the old.

Smith (1972) used the relationship between Murphy's (1966) sardine biomass estimates and the CalCOFI sardine larva censuses to calibrate the CalCOFI anchovy larva censuses. However, Murphy forced his cohort analysis results to agree with the CalCOFI sardine egg censuses, which are highly correlated with the sardine larva censuses. Therefore, the remarkably good relationship between Murphy's estimates and the CalCOFI sardine larva censuses (Figure 3) is somewhat artificial and is not a test of the validity of his biomass estimates. Actually, the relationship is much tighter than should be expected: Taft's (1960) analysis of CalCOFI sardine egg sampling indicated that the variance of a single cruise estimate increases with the mean, so that 95% confidence limits for the mean would be one-half to double the estimated value. Since temporal variability is also extreme, the season estimate is probably relatively less precise than single cruise estimates. Also, in comparing spawning products with cohort analysis abundance estimates, further variability is likely from environmental influences

Table 4
 CalCOFI Census of Pacific Sardine Larvae.

Year	TOTAL AREA (Smith 1972)		NORTH OF 30° N (Smith, personal communication)	
	census (10 ⁶ larvae)*	biomass/larva (10 ⁻³ tons/larva)	census (10 ⁶ larvae)	biomass/larva (10 ⁻³ tons/larva)
1951	2685	0.193	305	0.908
1952	2633	0.191	382	0.356
1953	2189	0.294	732	0.276
1954	3193	0.190	1361	0.176
1955	1959	0.197	1220	0.139
1956	1706	0.156	419	0.258
1957	1137	0.168	293	0.307
1958	1453	0.175	266	0.665
1959	570	0.302	219	0.557
1960	975		150	0.587
1961	642		67	0.806
1962	731		64	0.422
1963	379		248	0.085
1964	505		20	0.550
1965	1098		19	0.179
1966	735		31	
mean		0.207		0.418
standard deviation		0.053		0.251

*Smith (1972) erroneously used units of 10¹² larvae.

on spawning rates. Figure 3 shows none of these properties.

Although the recalculated sardine spawning biomasses are much lower than Murphy's for the period since 1950, the geographical area is also much smaller. For proper comparison, the CalCOFI censuses must also reflect this change in area, and therefore will also be considerably smaller than the previous values (Table 4). The revised relationship between larva censuses and estimated spawning biomass (Figure 4) shows much more scatter than did Smith's (1972) relationship; however, the pattern is very consistent with the sampling properties described by Taft (1960). When the logarithms of the variates are considered (Figure 5), the geometric mean (GM) regression (Ricker, 1973) slope is 0.973. This slope is reasonably close to the value of 1.0, which is characteristic of a proportional relationship between the untransformed variates and is a necessary quality of a good index. The error variance is constant for the log transformation, and the scatter about the regression is about twice Taft's "one-half to double" $s = 0.691$, 95% confidence limits are one-quarter to quadruple.)

Smith (1972) found the relationship

$$B = 0.206 L \quad (s = 0.053)$$

where B is sardine spawning biomass (million tons) from

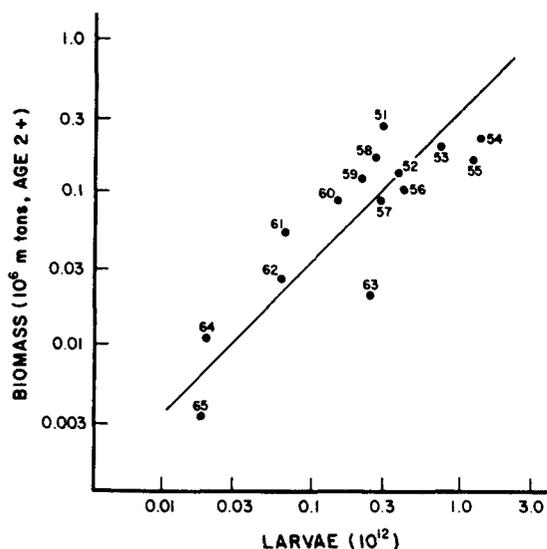


Figure 5. Revised relationship between sardine spawning biomass and CalCOFI sardine larva census, plotted on logarithmic scale.

cohort analysis, and L is CalCOFI larva census (10^9 larvae). The revised relationship (calculated as the mean of the ratios) is

$$B = 0.418 L \quad (s = 0.251)$$

or about double the previous estimate but with much less precision than was formerly attributed to the relationship. Because Smith's (1972) method of calibrating CalCOFI anchovy larva censuses only makes the assumption that anchovies are twice as fecund as sardines, without specifying either actual fecundity, his anchovy biomass estimates are unaffected by this change in sardine biomass calibration.

While showing a large amount of scatter, the CalCOFI sardine larva census estimates agree with the recalculated spawning biomass estimates as much as can reasonably be expected. In this case the cohort analysis was done in ignorance of the larva census values, and the relationship can be used as a validation of results.

Stock-Recruitment Relationship

At low biomass, sardines appear to be fully mature at age 2, but at large biomasses only some of the 2-year-olds are mature. For purposes of this discussion, spawning biomass will be calculated as all fish of age 2 or older, and any lost spawning potential at large biomasses will be subsumed in density-dependent characteristics of the stock-recruitment relationship. Recruitment can be compared with spawning biomass by using Murphy's concept of "potential spawning biomass," being the expected

spawning biomass of a year-class integrated over its lifetime, given particular mortality and growth rates. Murphy's calculation of potential spawning biomass will be modified here: all fish age 2 or older contribute, and the measure of initial year-class strength will be numbers of individuals at age 2 rather than biomass at age 2. The reason for the latter change is that calculation of biomass is dependent upon estimation of the mean weight of an individual in the year class. This, in turn, is strongly affected by the time of year in which most of the 2-year-olds are caught and is, therefore, subject to large and non-relevant sources of variation. Moreover, large fish at age 2 do not necessarily maintain a proportional weight advantage throughout the remainder of their lives. Weights at age are taken from Murphy's Table 16 and will be constant for all levels of biomass. Probable higher growth rates or condition factors when population size is low (MacGregor 1959) are ignored here but could result in as much as a 15% increase in spawning potential.

Previous analyses of the sardine stock-recruitment relationship (Clark and Marr 1955; Radovich 1962; Murphy 1966, 1967) showed density dependence, often by assuming a parabolic or Ricker functional relationship. There is sufficient scatter in the data to fit nearly any type of stock-recruitment function, with no way of determining the true relationship. Other information, such as the geographic composition of the stock (Radovich 1962), can be added to produce a plausible description of the stages in the historical collapse of the fishery. On the other hand, Cushing (1971) concluded that clupeoid stocks tend not to have strong density-dependent regulatory mechanisms, resulting in extreme natural variability and susceptibility to overfishing.

The Pacific sardine has experienced a thousand-fold decrease in abundance since 1932, which makes it necessary to condense the stock-recruitment observations by use of log transformations (Figure 6). Diagonals representing replacement under different fishing mortality rates are plotted for reference. Contrary to previous analyses of the stock-recruitment relationship, this plot shows no functional density-dependent trends whatsoever and agrees with the position of Cushing (1971). There is no increase in recruitment strength relative to parental biomass at low stock sizes, and at every stock size before 1960, recruitments are evenly distributed about the replacement line if there is no fishing mortality. As fishing mortality rate increases, fewer spawnings exceed replacement strength, indicating very little resilience of the population to fishing pressure. For the years 1932 to 1959, the mean replacement success, as measured by $\ln R - \ln P$, is only 0.11, or 12% above replacement at no fishing mortality (the arithmetic mean would be slightly larger). Since year-classes persist for several years and strong year-classes are arithmetically stronger than their loga-

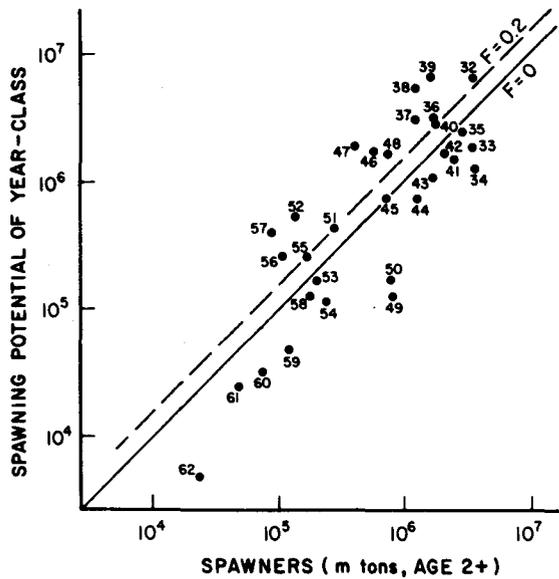


Figure 6. Stock-recruitment relationship of sardine plotted on logarithmic scale.

hythmic values suggest, the reproductive potential may be somewhat higher than the above analysis would conclude. Also, successful reproduction seems to occur in sequences of several years' duration, followed by similar runs of poor reproduction. The duration and timing of these runs has a large effect on potential population growth over long periods of time. These factors will be evaluated by simulation in the next section.

The string of poor recruitments since 1958 is remarkable in its duration and magnitude. The most likely explanation is that the high fishing pressure of the 1950's decimated the northern stock to the point where immigration from the southern stock was making up a large portion of the commercial catch. Consequently, estimates of the size of the northern stock are inflated for purposes of estimating its spawning potential (although they may be fairly realistic as a measure of biomass available to the fishery). Presumably, fish of southern origin are less likely to spawn in the cool waters off California. The record since 1958 is not necessarily a series of spawning failures but may be a series of overestimated spawning biomasses for the northern stock.

Population Simulations

Simulation models of the Pacific sardine stock have been used to answer questions relating to management strategies (Lenarz 1971) and to probable futures of the population (Murphy 1967). These simulations employed the Ricker stock-recruitment relationship given by

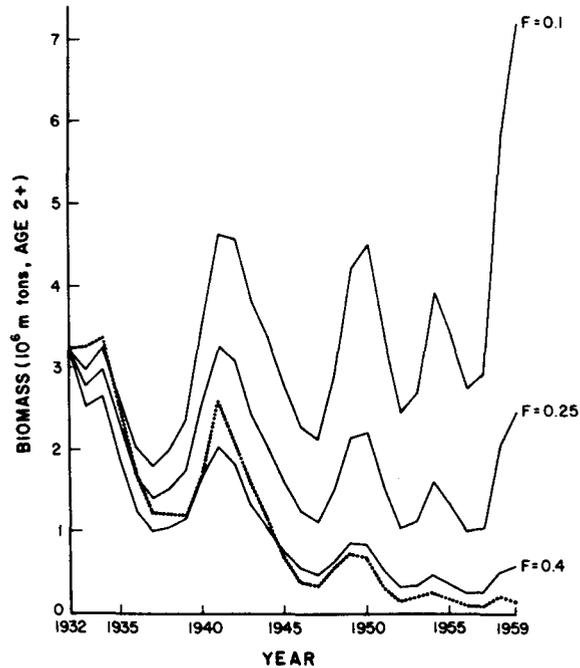


Figure 7. Sardine population simulation results for various rates of constant fishing mortality rates.

Murphy (1966) and reflect the production characteristics of that curve. If the functional stock-recruitment relationship is virtually linear, as is suggested in this paper, the previous simulations are unrealistic and contain a tendency toward an equilibrium which may not, in fact, exist.

The effects of two simple management strategies, constant fishing mortality rate and constant quota, will be examined as they would have affected the actual population from 1932 to 1959, the last potentially peak year of population size. The simulation model recreates annual population age compositions based on spawning rates and natural mortality rates as they historically occurred. Fishing mortality rates (determined by management strategy) are the only source of variation in the model: all other elements are fixed. Observed spawning rates, measured as recruits at age 2 per parental biomass age 2 and older, are employed directly. This method of simulating recruitment makes few assumptions as to the true nature of the stock-recruitment relationship. If any density-dependent compensation actually occurs in this relationship, those simulated will tend to be "optimistic" when the simulated population is larger than the actual population from which the spawning rates were obtained. The simulation begins with the age distribution in 1932 given by Murphy (1966, Table 14) and uses the constant weights at age given in his Table 16. Fish of age

3 and greater are treated as fully recruited to the fishery, and age-2 fish are 50% recruited, suffering one-half the instantaneous fishing mortality rate applying to older fish. A natural mortality rate of $M = 0.4$ is assumed for all ages.

The first simulation (Figure 7) examines population trends under three levels of constant fishing pressure: $F = 0.1$, 0.25 , and 0.4 . The first value allows slow growth, with the population jumping to unreasonably high biomasses in 1958 and 1959 due to the high spawning rates of 1956 and 1957. The second value of $F = 0.25$ causes the population to decline slowly from its peak in the early 1930's, maintaining biomasses between one and two million tons. The third value causes the population to decline to very low levels of about one-half million tons, which must be considered suboptimal. The biomass fell to even lower levels under the actual fishery, giving the simulations an upward bias except for the first few years when the fishing pressure was light and the actual population was larger than the simulation. Thus it appears that $F = 0.25$ is about the maximum constant-fishing pressure that the sardine fishery could have sustained.

An interesting but unrealistic simulation is that of $F = 0$, simulating the growth rate resulting from observed recruitment rates unhindered by fishing or environmental limitation. If the stock-recruitment relationship actually has little or no density-dependent compensation (except at very large population sizes), this growth rate is an approximation of the intrinsic rate of increase (r) in the natural environment. The slope of the logarithm of these simulated population sizes versus time gives an r of 0.082 (8.5%/year). This is considerably less than Murphy's (1967) value of $r = 0.338$, which was based on an extrapolation of his assumed, highly density-dependent Ricker stock recruitment curve to a theoretical zero biomass.

The second simulation holds the annual catch of the fishery constant, approximating a constant-quota system (Figure 8). The simulated population is able to maintain its biomass under a quota of 300,000 metric tons annually but is unable to maintain a quota of 350,000 tons. Due to the "optimistic" bias of the simulation, a safer estimate of maximum sustained yield (MSY) would be 250,000 tons annually. Murphy's (1966) estimate of MSY was 427,000 metric tons (471,000 short tons), which does not seem to have actually been sustainable. The extreme sensitivity of a naturally fluctuating resource to small changes in quota levels indicates the danger of basing management on such an inflexible system. A program of reduction or cessation of fishing at low biomasses is necessary to provide protection from collapse of an easily overfished resource.

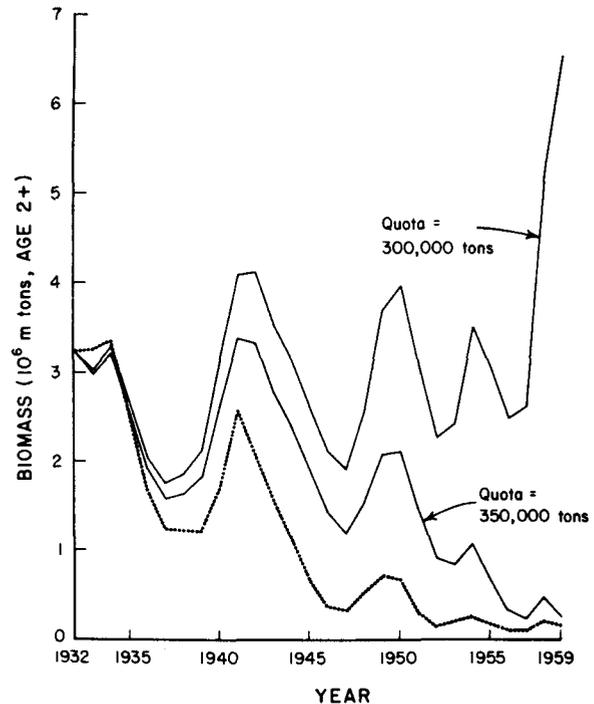


Figure 8. Sardine population simulation results for two levels of annual catch quotas.

This estimate of maximum sustainable yield from the sardine fishery is much smaller than the Gulland potential-yield estimate (Gulland 1970) would give. Using a natural mortality rate of $M = 0.4$ and using the 1932 biomass of 3.2 million metric tons as an estimate of virgin fishable biomass (B_0), potential yield (C_{max}) is estimated to be $0.5 \times 0.4 \times 3.2$ million tons, or 640,000 tons. This is two and one-half times larger than the simulation result and clearly would not be sustainable. The Gulland potential yield estimator appears to require further modification in the case of a naturally fluctuating stock, which may have little density-dependent regulation of recruitment. Two modifications may be suggested: either use as B_0 the smallest population size that has been observed in the virgin state, or use one-half of the Gulland potential yield as a more realistic estimate. For example, the Gulland potential yield from the northern anchovy (*Engraulis mordax*) central stock has been estimated as one to two million tons (MacCall et al. 1976). One-half of this estimate is 500,000 to 1,000,000 tons, which is much closer to estimates of surplus production based on observed growth rates of the population (Radovich and MacCall, this volume), which project an anchovy MSY of approximately 450,000 tons.

CONCLUSIONS

1. A new time series of biomass estimates for Pacific sardine extending to 1963 is presented, based on a cohort analysis of catches from the geographical area associated with the northern stock. The new population estimates are considerably smaller than those previously published and are, moreover, in better agreement with trends in independent indices of abundance (catch per unit effort, night-light surveys) for California waters.

2. It is not necessary to assume an increase in rate of natural mortality from $M = 0.4$ to $M = 0.8$ in the 1950's to obtain reasonable biomass estimates.

3. A decrease in the relative abundance of 2- and 3-year-old fish occurred in the 1950's, possibly reflecting a progressively southerly origin of year classes. Failure to recognize this change caused a downward bias in previously published estimates of fishing mortality rates for the 1950's, wherein 3-year-old fish were assumed to be fully recruited.

4. The ratio of sardine spawning biomass to CalCOFI sardine larva census is double the previous value. A 95% confidence interval ranges from one-quarter to quadruple the estimated biomass. The relationship displays the expected statistical qualities, whereas the previously published relationship was artificially precise.

5. A purely functional description of the stock-recruitment relationship since 1932 shows no curvature (density-dependent regulation of recruitment), indicating little resilience to fishing. Had there been no fishing, the stock would, on the average, have done little better than replace itself. The average potential growth rate appears to have been 8.5%/year, with large fluctuations.

6. The apparently poor rates of recruitment in the 1960's are likely to be the result of including immigrant fish from the southern genetic group in estimates of spawning biomass of the northern stock. These southern fish may not be adapted to spawning in the relatively cool waters off California. Recruitment rates of the remaining fish from the northern genetic group may have been quite normal.

7. A simulation model of the sardine population containing "optimistic" biases showed the maximum continuous-fishing mortality rate that the sardine population could have sustained to have been $F = 0.25$ (22% annually).

8. The same model showed that the population could have sustained a constant annual quota of 300,000 metric tons but would have been seriously depleted by a 350,000 ton quota. Due to instability induced by a constant harvest from a fluctuating population, and to the "optimistic" bias of the model, maximum sustained yield for the northern stock was probably about 250,000 tons. This estimate is considerably lower than the previous estimate of 427,000 metric tons (Murphy 1966).

9. The Gulland potential yield estimation (Gulland 1970) would have estimated potential maximum sustained yield to be 640,000 metric tons, which would not have been sustainable. The Gulland estimator may have to be revised downward in the case of populations subject to large natural fluctuations in abundance.

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REFERENCES

- Blunt, C.E., and M. Kimura. 1966. Age, length composition, and catch localities of sardine landings on the Pacific coast of the United States and Mexico in 1963-64. *Calif. Fish Game*, 52: 133-150.
- _____. 1971. Age composition of sardine landings on the Pacific coast of the United States and Mexico in 1965-66. *Calif. Fish Game*, 57: 202-204.
- Clark, F.N. 1956. Average lunar month catch of sardine fishermen in southern California, 1932-1933 through 1954-1955. *Calif. Fish Game*, 42: 309-322.
- Clark, F.N., and J.C. Marr. 1955. Population dynamics of Pacific sardine. *Calif. Coop. Oceanic Fish. Invest., Prog. Rep.*, July 1, 1953-March 31, 1955: 11-48.
- Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. *J. Cons. Int. Explor. Mer*, 33: 340-362.
- Daugherty, A.E., and R.S. Wolf. 1964. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1961-62. *Calif. Fish Game*, 50: 241-252.
- Felin, F.E. 1954. Population heterogeneity in the Pacific pilchard. *U.S. Fish Wildl. Serv., Fish. Bull.*, 86: 201-255.
- Gulland, J.A. 1970. The fish resource of the ocean. *FAO Fish. Tech. Pap.* 97: 1-425.
- Jones, R. 1961. The assessment of the long-term effects of changes in gear selectivity and fishing effort. *Mar. Res. (Scotland)*, 1961(2): 1-19.
- Kimura, M., and C.E. Blunt. 1967. Age, length composition, and catch localities of sardine landings on the Pacific coast of the United States and Mexico in 1962-63. *Calif. Fish Game*, 53: 105-124.
- _____. 1971. Age composition of sardine landings on the Pacific coast of the United States and Mexico in 1964-65. *Calif. Fish Game*, 57: 107-112.
- Klingbeil, R.A. 1974. Average lunar monthly catch of sardines in California for the 1954-55 through 1961-62 seasons. *Calif. Dept. Fish Game, Mar. Res. Tech. Rep.* 26: 43p.
- Knaggs, E.H. 1972. San Pedro wetfish fleet: major purse-seine gear changes 1952-1972. *Commer. Fish. Rev.*, 34(5): 11-32.
- Kramer, D. 1970. Distributional atlas of fish eggs and larvae in the California Current region: Pacific sardine, *Sardinops caerulea* (Girard), 1951 through 1966. *Calif. Coop. Oceanic Fish. Invest., Atlas No.* 12: 277p.
- Lenarz, W.H. 1971. Modelling the resource base. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 15: 28-32.
- MacCall, A.D. 1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 18: 136-148.

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CalCOFI Rep., Vol. XX, 1979

- MacCall, A.D., G.D. Stauffer, and J.P. Troadec. 1976. Southern California recreational and commercial marine fisheries. *Mar. Fish. Rev.*, 38(1): 1-32.
- MacGregor, J.S. 1959. Relation between fish condition and population size in the sardine (*Sardinops caerulea*). U.S. Fish Wild. Serv., Fish. Bull. 166, 60: 215-230.
- Murphy, G.I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). *Proc. Calif. Acad. Sci.*, 34(1): 1-84.
- _____. 1967. Vital statistics of the Pacific sardine (*Sardinops caerulea*). *Ecology*, 48: 731-736.
- Radovich, J. 1962. Effects of sardine spawning stock size and environment on year class production. *Calif. Fish Game*, 48: 123-140.
- Radovich, J., and A.D. MacCall. 1979. A management model for the central stock of the northern anchovy, *Engraulis mordax*. *Calif. Coop. Oceanic Fish. Invest. Rep.* (this volume).
- Ricker, W.E. 1973. Linear regressions in fishery research. *J. Fish. Res. Board Can.*, 30: 409-434.
- Smith, P.E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. *Fish. Bull., U.S.*, 70: 849-874.
- Taft, B.A. 1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. *Limnol. Oceanogr.*, 5: 245-264.
- Tomlinson, P.K. 1970. A generalization of the Murphy catch equation. *J. Fish. Res. Board Can.*, 27: 821-825.
- Wolf, R.S. 1961. Age composition of the Pacific sardine. U.S. Fish Wildl. Serv., Res. Rep., 53: 1-36.